

TEMPORAL STRUCTURE OF PERCEPTUAL GROUPING: EEG ANALYSIS

Andrey R. Nikolaev^{a,b}, Sergei Gepshtein^a, Michael Kubovy^c, and Cees van Leeuwen^a

^a RIKEN Brain Science Institute, 2-1 Hirosawa, Wako-shi, 351-0198, Japan

^b Institute of Higher Nervous Activity, Butlerov str., 5a, Moscow, 117485, Russia

^c Department of Psychology, PO Box 400400, University of Virginia, Charlottesville, VA, USA

Abstract

We studied pre- and post-stimulus scalp-recorded electrical brain activity during perceptual grouping. Observers reported the orientations of perceived dot groupings in multistable dot lattices. We varied lattice ambiguity and orientation. Observer reports showed a bias for vertical orientation. This bias was reflected in the cortical alpha activity before stimulus onset: the tendency to see vertical groupings corresponded to low pre-stimulus alpha power. In the post-stimulus evoked activity we found that observers' grouping sensitivity was positively correlated with the amplitude of the earliest event-related peak, C1 (about 60 ms after stimulus onset) and negatively correlated with the amplitude of the following peak P1 (about 110 ms). The dissociation of two early brain activities is evidence of two separate early mechanisms serving perceptual grouping: one mechanism reflects individual grouping sensitivity, while the other reflects the modulation of this sensitivity by top-down influences.

This study deals with a particular form of perceptual organization – grouping by proximity – which is a classical Gestalt factor of perceptual organization (Wertheimer, 1912). Our approach combined two methods: One is a *phenomenological report paradigm*, in which multi-stable dot lattices are presented for measuring perceptual grouping by proximity (Kubovy, 1994; Gepshtein & Kubovy, 2005). The other is high-density *electroencephalography* (EEG) for the study of cortical chronometry. Combining the power of the phenomenological report method with the temporal sensitivity of EEG allowed us to measure grouping ability more precisely than in previous studies of perceptual grouping using EEG (e.g., Han, Song, Ding, Yund, & Woods, 2001). By recording post-stimulus evoked cortical activity together with observer reports for graded stimuli we identified systematic changes in cortical activity, reflecting grouping strength. We also recorded ongoing EEG activity that preceded stimulus presentation and found that this activity predicted the “orientation bias” of perceptual grouping, which is the preference of groupings aligned with a certain orientation in the world coordinates (Gepshtein & Kubovy, 2005).

Method

Experiment 1

Seventeen healthy observers (ages 19-36, median age 22, 9 women) took part in the experiment. We used multistable dot lattices, each of which appeared to be grouped into strips of dots (Kubovy, 1994). The perceived organization of a dot lattice depends on its aspect ratio (AR), which is the ratio of the two shortest inter-dot distances. We used four different values of AR: 1.0, 1.1, 1.2, and 1.3 (Fig. 1A). The lattices were presented at four different orientations, in which the orientation of shortest inter-dot distance was rotated counterclockwise from the horizontal for 22.5, 67.5, 112.5, or 157.5°. The four aspect ratios and four orientations yielded 16 different stimuli. Within each experimental block each of the 16 conditions was presented 10 times in a random order. Four such blocks were presented to every observer. The diameter of the dots was 0.2° of visual angle. The distances between dot centers at AR=1.0 were 0.6° of visual angle. Observers sat 1.15 m from the screen in a dimly lit room.

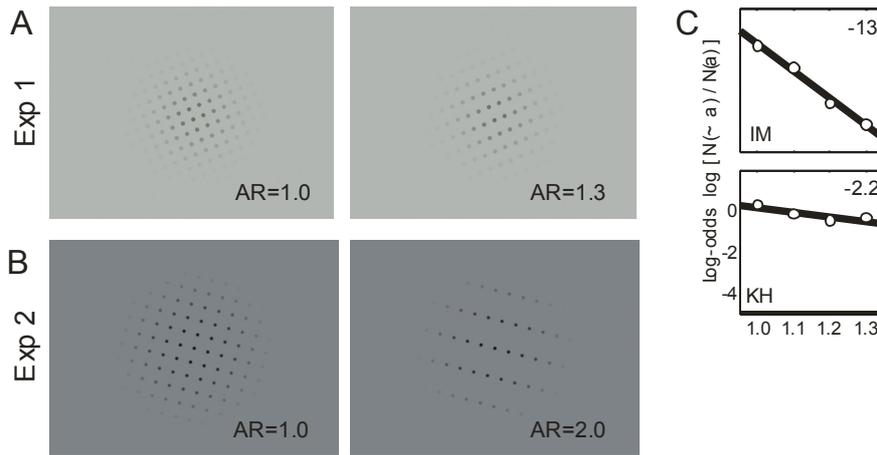


Fig 1: A. Dot lattices used in Experiment 1 with aspect ratios (ARs) 1.0 and 1.3 (ARs 1.1 and 1.2 are not shown). B. Dot lattices used in Experiment 2. (ARs: 1.0 and 2.0) C. The log-odds of responses vs. lattice aspect ratios in Experiment 1. $N(a)$ are the responses indicating that observers saw the moist likely organization and $N(\sim a)$ are the all other responses. The slopes of linear fits represent observer's grouping sensitivity: of the 13 observers we show data for one with the highest (slope -13) and one with the lowest (-2.2) sensitivities.

Each trial consisted of four intervals: fixation, stimulus, blank screen, and response screen. The duration of the stimulus interval and the blank-screen interval were both fixed at 300 ms. A response screen (four icons depicting the orientations of most likely dot groupings) was presented until a response was received. The observers' task was to report the orientation of the perceived grouping by clicking on the corresponding icon. We explained to the observers that the task had no correct or incorrect answer.

EEG was recorded using a 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR). Post-stimulus activity (event-related potentials; ERP) was analyzed as follows. We filtered the EEG signal using a wide-band 0.3-25 Hz filter. The data were segmented into 500 ms epochs, including 100 ms before and 400 ms after stimulus onset. We ran an automatic artifact detection procedure. Data from two observers having more than 33% artifact epochs were excluded from further analysis. Single trials were averaged separately for each observer and each condition. The data were average-referenced and baseline-corrected relative to a 100-ms interval prior to stimulus onset. Because of the short stimulus duration, we analyzed only the amplitudes of early ERP peaks: C1 (60-90 ms after stimulus onset) and P1 (100-150 ms). On the grand-average maps we located areas of voltage maxima (or minima) for each peak. Then we selected groups of adjacent channels in which the peak values were within $0.3 \mu\text{V}$ from the maximal or minimal values. For each observer the peaks were searched within 50-ms windows centered on the grand-average peaks C1 and P1.

Pre-stimulus activity was evaluated in single trials during the 1 s preceding stimulus presentation. We calculated the mean power of alpha activity in 8-13 Hz in 59 electrodes over occipital areas and then averaged the power across electrodes.

Experiment 2

This experiment had two goals. First, we sought to support our results from Experiment 1 in a different group of observers, because the amplitudes of early ERP peaks (such as C1) are generally very low. Second, we asked how a larger range of aspect ratio would affect brain activity: now we used aspect ratios 1.0 and 2.0 (Fig. 1B).

Nine healthy observers (ages 19-33, mean age 23.5, six women) took part in the experiment. Lattice orientations were: 15, 30, 60, 75, 105, 120, 150, and 165° counterclockwise from the horizontal. For AR=2.0, the rotations yielded 8 stimuli, whereas

for AR=1.0 the rotations yielded 4 stimuli (because orthogonal rotations of AR=1.0 correspond to the same orientations). The stimuli were presented in a random order in blocks of 192 trials. We analyzed only the post-stimulus ERP activity. Other details were as in Experiment 1.

Results and Discussion

Behavioral results

Experiment 1

In Fig. 1C we plot log-odds of responses vs. lattice aspect ratios. The slope of the linear fit for every observer is a measure of his or her performance in the grouping task, which we call *grouping sensitivity*. We quantify grouping sensitivity using the absolute value of the slope: the higher the slope magnitude the better grouping performance. We excluded two observers from the analysis because they were unable to perform the task adequately. We divided the remaining 13 observers into two groups: “high sensitivity” (6 observers) and “low sensitivity” (7 observers).

We evaluated observers’ orientation bias by calculating the ratio of reports of an orientation to the total number of possible reports of the given orientation (excluding AR=1.0). We compared this ratio across four orientations in the group of 13 observers. A repeated-measures ANOVA revealed an effect of orientation ($F(3, 36) = 13.7, p < 0.001, \epsilon = 0.57$) (Fig. 4A). A post-hoc Tukey HSD test showed that close-to-vertical orientations (67.5° and 112.5°) were reported more frequently than close-to-horizontal orientations (22.5° and 157.5°) (all $p < 0.01$).

Experiment 2

With biased lattices (AR=2.0), observers predominantly reported seeing orientations along the shortest inter-dot distance ($96.6 \pm 2.2\%$). Other organizations were reported in $2.3 \pm 1.7\%$ of trials across observers, excluding one observer who reported seeing organizations along the longer inter-dot distances in 40% of trials. In the ambiguous lattices (AR=1.0) the two most likely organizations were seen with equal frequency (43.2 ± 5.7 and $44.3 \pm 6.1\%$), while the two other organizations were reported in $12.5 \pm 9.3\%$.

EEG results

Experiment 1

Negative peak C1 (latency 55 ms, SEM 1.2 ms) was prominent in the middle occipital areas. A 4x4 ANOVA of the amplitude of this peak (factors Aspect Ratio vs. Orientation) failed to reveal significant effects in the group of all observers. In the high-sensitivity group, however, the ANOVA revealed an effect of aspect ratio ($F(3, 15) = 4.3, p < 0.05, \epsilon = 0.84$) (Fig. 2A, B). We also observed a weak effect of orientation ($F(3, 15) = 3.0, p = 0.09, \epsilon = 0.71$). The interaction was not significant. In the low-sensitivity group, we found neither effects nor an interaction (Fig. 2C, D). The post-hoc Tukey HSD test showed that the effect of aspect ratio was prominent mostly because of a larger amplitude of C1 at AR=1.0 than at AR=1.1 ($p < 0.05$) and AR=1.3 ($p < 0.05$) (Fig. 2A). This implies that the less biased was the stimuli (i.e., the smaller was AR), the more negative was the amplitude of C1. The post-hoc test showed that the effect of Orientation was explained by a larger C1 amplitude at orientation 157.5° than 22.5° ($p < 0.01$), although the effect of orientation on peak amplitude was graded.

Positive peak P1 (latency 108 ms, SEM 4.8 ms) was prominent in posterior lateral occipital areas. In contrast to peak C1, we found effects of aspect ratio on this peak in all observers. A 4x4 ANOVA on P1 amplitude revealed a significant effect of aspect ratio ($F(3, 36) = 3.7, p < 0.05, \epsilon = 0.79$). Neither the effect of orientation nor the interaction was significant. A post-hoc test revealed that the effect of aspect ratio was prominent mostly

because of the higher P1 amplitude at AR= 1.3 than at AR=1.0 ($p < 0.05$) and AR=1.2 ($p=0.06$). In other words, larger aspect ratios evoked larger amplitude of P1. This result is opposite to the effect of aspect ratio on the amplitude of C1.

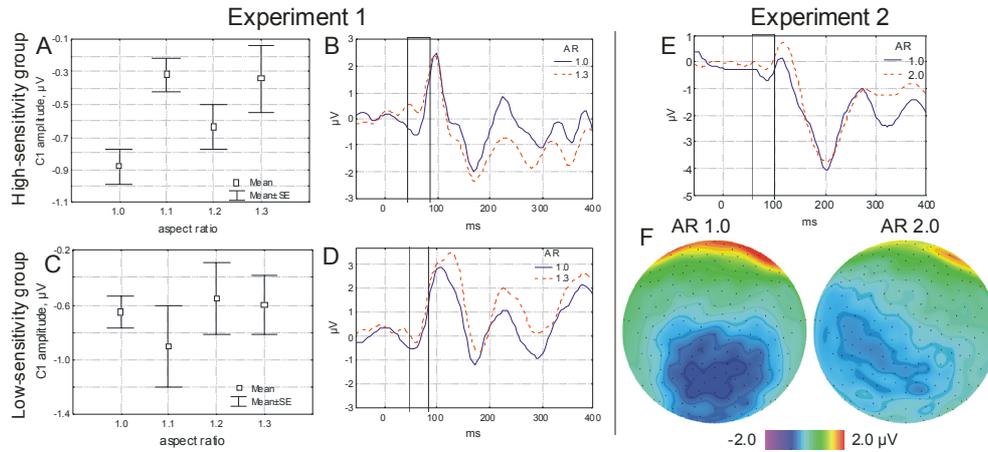


Fig 2: Effect of aspect ratio on peak C1. Experiment 1: A and C. Mean-error plots of C1 amplitude across aspect ratios in the high-sensitivity (A) and low-sensitivity (C) groups. B and D. Grand-average ERPs in the representative channel from the middle occipital areas for the high-sensitivity (B) and low-sensitivity (D) groups for aspect ratios 1.0 and 1.3. Experiment 2: E. Grand-average ERPs for aspect ratios 1.0 and 2.0. F. Grand-average voltage maps for peak C1 for aspect ratios 1.0 and 2.0.

Different roles of C1 and P1 activity in perceptual grouping

The differences between the low- and high-sensitivity groups suggest a systematic relationship between grouping sensitivity and the amplitude of peaks C1 and P1. To further investigate this effect we calculated the differences $-\Delta C1$ and $\Delta P1$ – between the amplitudes of the two peaks at AR=1.0 and AR=1.3 (extreme values of aspect ratio) for each orientation, and then averaged the magnitudes of $\Delta C1$ and $\Delta P1$ across orientations. Using a general linear regression model we measured a multivariate association between grouping sensitivity and $\Delta C1$ and $\Delta P1$. Wilks multivariate test showed that the association was significant (Wilks $\lambda=0.30$, $F(4,8)=4.6$, $p < 0.05$). Estimation of regression coefficients revealed a significant correlation with $\Delta C1$: 0.62 ($p < 0.05$) (Fig. 3).

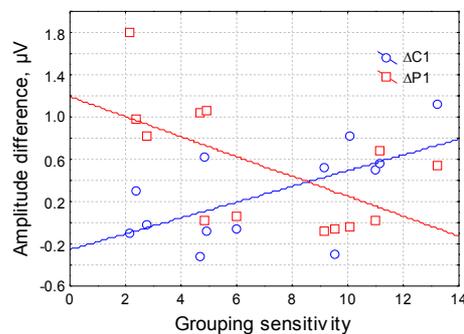


Fig 3: Correlation between grouping sensitivity and the effects of aspect ratio on cortical activity. Each point represents one observer.

That is, the higher was grouping sensitivity the greater was the effect of stimulus aspect ratio on the amplitude of C1. For $\Delta P1$, the correlation coefficient was -0.60 ($p < 0.05$). The negative correlation means that a larger $\Delta P1$ corresponded to a lower grouping sensitivity.

Thus, we found that the correlations between grouping sensitivity and the effect of AR on peak C1 and P1 had the opposite signs. The dissociation between these two earliest ERP events suggests that they correspond to processes that play different roles in perceptual grouping, as we discuss below.

Pre-stimulus activity

We sorted single trials of pre-stimulus alpha power in four groups corresponding to the four orientations of potential groupings. For each orientation we averaged the alpha power in each observer. A repeated-measures ANOVA in the group of 13 observers revealed significant effect of orientation on alpha power ($F(3, 36) = 5.0, p < 0.01, \epsilon = 0.96$) (Fig. 4B). Post-hoc test showed that the effect was mainly due to a higher power in the close-to-horizontal orientation 157.5° ($p=0.01$). Remarkably, magnitudes of alpha power in close-to-vertical orientations 67.5° and 112.5° were nearly identical ($p=0.999$). Thus, vertical orientation bias was prominent in trials with low pre-stimulus alpha power. In other words, pre-stimulus alpha activity was a reliable predictor of orientation bias.

Experiment 2

The amplitude of peak C1 (latency 79 ms, SEM 6.9 ms) was significantly more negative at AR=1.0 ($-1.3 \mu\text{V}$, SEM=0.2) than at AR=2.0 ($-0.7 \mu\text{V}$, SEM=0.2; $t = 2.7$; $p < 0.05$) (Fig. 2E). This result, which here holds for all observers, corresponds to that of the high-sensitivity observers in Experiment 1. The C1 negativity at AR=1.0 was most prominent in the middle occipital region, which is an approximate projection of the primary visual areas on the scalp (Fig. 2F). Experiment 2 confirmed in a different group of observers the finding of Experiment 1 that stimulus parameters affect cortical activity as early as the first ERP peak. The confirmation is valuable because peak C1 has low amplitude, which makes it difficult to detect modulations of this peak by stimulus parameters. As in Experiment 1, the lowest amplitude of C1 was observed at the lowest aspect ratio (AR=1.0). Remarkably, the difference between C1 amplitude observed in AR=1.0 and the highest C1 amplitude obtained in each experiment (observed in 1.3 in Experiment 1 and in 2.0 in Experiment 2) was nearly the same in both experiments: about $0.6 \mu\text{V}$. This suggests that at AR=1.3 the effect of aspect ratio on the amplitude of C1 was saturated, such that further improvements in performance are not reflected in C1 activity. It is also likely that in Experiment 2 the effect was saturated in high-sensitivity observers, but for the low-sensitivity observers the larger difference in AR compensated for their lack of sensitivity.

The effect of aspect ratio on peak P1 (mean latency 120 ms, SEM=10.7 ms) was not significant. This is surprising because we found such an effect in Experiment 1. The choice of stimuli may explain the different results: the large differences between stimulus aspect ratios may reduce the later effect, as we explain below.

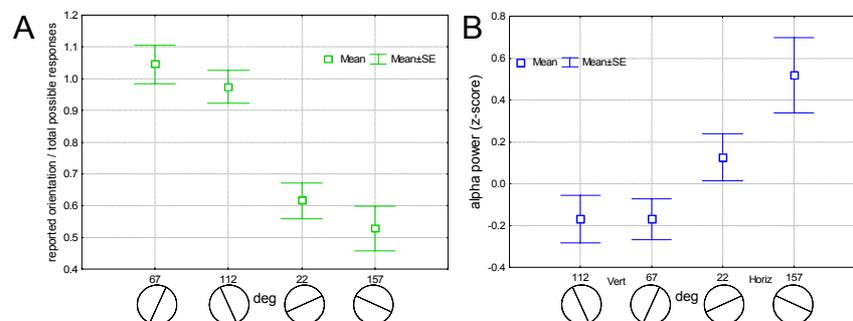


Fig 4: A. The ratio of reports of an orientation to the total number of possible reports of the given orientation for each orientation. There is a strong bias to vertical orientations. B. Pre-stimulus alpha power for each reported orientation.

Summary

To summarize, in the analysis of post-stimulus brain activity we found dissociation between the two earliest cortical events evoked by dot lattices in a grouping task. *First*, we found a reliable effect of aspect ratio on cortical activity as early as 55 ms after stimulus onset (peak C1). This effect predicted observer's ability for perceptual grouping: the greater the effect the greater the grouping ability. C1 activity is generally attributed to feed-forward visual processes that precede awareness. Spatial-frequency analysis of visual stimuli is one of these processes. It was found that the larger was high spatial-frequency power of the stimulus the higher was C1 amplitude (Kenemans, Kok, & Smulders, 1993), in agreement with our results. *Second*, we found a reliable relationship between grouping sensitivity and the next cortical event – peak P1 (108 ms after stimulus onset), but this relationship had an opposite direction: the greater the effect of aspect ratio the lower the grouping ability. P1 is generally attributed to lateral and feedback cortical interactions associated with perceptual awareness and attention. The absence of the effect of aspect ratio on amplitude of P1 in Experiment 2 is consistent with this interpretation: the large difference between aspect ratios in that experiment probably reduced the need for top-down mediation. The dissociation of C1 and P1 activities suggests that they represent different mechanisms of perceptual grouping: one mechanism is responsible for grouping sensitivity, while the other mechanism constitutes a top-down modulation of this sensitivity.

In the analysis of ongoing cortical activity we found that the alpha power of pre-stimulus activity predicted a bias in observer reports of grouping orientation: Most observers preferred vertical groupings to groupings in other orientations. The vertical bias corresponded to a lower pre-stimulus alpha power. The bias mostly affected observer reports when dot lattices were perceived against stimulus support, i.e., were inconsistent with the proximity principle. The orientation bias may originate in intrinsic properties of ongoing cortical dynamics: results of optical imaging of monkey cortex showed that in the “eyes closed” condition the ongoing cortical activity spontaneously formed orientation-specific patterns similar to the patterns evoked by orientated stimuli when the eyes were open (Kenet, Bibitchkov, Tsodyks, Grinvald, & Arieli, 2003). If similar activity existed in human visual cortex, it might constitute the biological mechanism of orientation bias, so the statistical properties of that activity would correspond to the statistical properties of perceptual bias.

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